

## Studies on the Turbellaria.

By

**W. A. Haswell, M.A., D.Sc., F.R.S.,**

Challis Professor of Biology, University of Sydney.

PARTS I AND II.

With Plates 25—27.

### Part I.—On *Heterochærus*, an “Acœlous” Turbellarian.

Introductory—Occurrence—External Features—Movements.—The genus *Amphichærus* was founded by von Graff (15) for a species previously (13) named by him *Convoluta cinerea*. A nearly allied North American form was described in 1892 by E. L. Mark (20), and further details of its structure, with an account of its development, were subsequently published by Gardiner (9 and 10).

The feature which was originally supposed to distinguish *Amphichærus* from all other members of the family (*Aphanostomida*) to which it belongs, was the presence of a bursa seminalis containing two chitinous “mouth-pieces,” but forms nearly related to *A. cinereus*, and regarded as referable to the same genus, have been found by von Graff (16) to possess a number of such chitinous parts. *Polychærus*, the genus described by Mark, has many chitinous mouth-pieces in the bursa, but it differs from all the known species of *Amphichærus* in having distinct vitellaria. In this latter point the form to be now dealt with differs from *Polychærus*, and agrees with *Amphichærus*, but in the

absence of a "frontal organ," as well as, probably, in other points, differs so widely from the other members of the group that it requires to be designated by a new generic name. I propose to call it *Heterochærus*, and the species *H. australis*.

It occurs in shallow rock-pools between tidal limits in Port Jackson towards high-water mark, and is most abundant in places in which it is exposed all day, without shelter of any kind, to the full glare of the sun. The breeding period extends throughout the summer and autumn months—November to May—specimens collected in October were sexually immature, while in June the sexual apparatus apparently undergoes degeneration, and soon practically disappears.

The worms were best fixed by running the water off them, and subjecting them in an almost dry condition to the action of the vapour of osmic acid. This kills most of them very soon without producing much contraction. They may then be treated with Flemming's strong chromosmic-acetic solution or with Hermann's solution, or with a picro-acetic-osmic solution. Hermann's solution, followed by Merkel's, gave some good results, but on the whole the picro-acetic-osmic combination was the most successful. Solutions containing sublimate (including Lang's and Gibson's formulæ) did not yield satisfactory results. Sabussow's (24) modification of Kultschitzky's photoxylin-paraffin method, with some alterations, proved entirely satisfactory for this brittle class of objects.

The largest specimens are about 4 mm. in length, 1.5 mm. in greatest breadth. The body (fig. 1) is compressed dorso-ventrally, thickish towards the middle line, thin at the sides, tapering to a blunt point in front, deeply excavated behind, and frequently unsymmetrical. Only in one case, among the very numerous specimens examined, have I found the thin lateral margins folded back on the dorsal surface after the fashion which prevails in *Convoluta*.

Locomotion may be effected by steady gliding through the water, usually in close contact with the solid substratum,

except that the head end is very frequently raised, sometimes in mid-water, by the agency of the cilia. When the movement is more rapid it is brought about by rhythmical undulations, in which the thin lateral flanges and the pointed anterior regions take the leading part; by means of similar movements the animal is able to swim rapidly in mid-water. As the animal moves along the anterior region is turned about actively in all directions, probing and testing, and seems to be by far the most sensitive part, responding with great rapidity to contact with foreign bodies—contact with other individuals of the same species causing a particularly active recoil often followed by what appears like a rapid aggressive movement. When at rest the anterior and lateral parts, together with the posterior processes, alone adhere to the surface, the body being somewhat arched in such a way that there is a wide space below into which the mouth and reproductive apertures open—the space communicating with the exterior freely behind between the posterior processes.

There is no frontal organ, such as occurs in most other *Acœla*.<sup>1</sup>

The mouth, a short longitudinal slit, is situated towards the middle of the ventral surface. Behind it are the two median reproductive apertures, the female in front and the male behind, separated from one another by a space which is considerably less than that separating the anterior from the mouth, the posterior separated from the posterior border by an interval slightly longer than that which intervenes between the female aperture and the mouth. There is a pair of minute eyes towards the anterior end, and an otocyst situated between them. In a mature animal the vesicula seminalis projects as a rounded prominence on the dorsal surface near the posterior border, and in front of this, also on the dorsal surface, is a well-marked depression marking the position of the aperture of the supposed Laurer's canal.

The colour, which varies greatly, depends partly on the symbiotic *Algæ* present, partly on pigment in the epidermis.

<sup>1</sup> Not in *Haplodiscus ussowii*, according to Sabussow (24).

The pigment is arranged in the form of a network of glistening narrow threads which lie immediately below the surface.

In some full-grown specimens it occurs in relatively small amount, and such specimens may appear of a uniform green or brownish-green colour. Usually the largest specimens are the darkest in colour.

The general coloration produced by the presence of the symbiotic Algæ and of pigment of various hues is a mottling of green, brown, and yellowish white, but the pattern which results is subject to endless variation. Very commonly there is a light (yellowish) spot over the region in front of the eyes and otocyst, and one on each side just behind, but this arrangement is by no means invariable. The whole animal is usually very opaque, and it is in most instances impossible to make out any part of the internal organisation of an entire living adult specimen. The opacity is due partly to the pigment and the symbiotic Algæ, partly to the presence of numerous drops of oily matter in the protoplasm of the cells. When the animals are looked at under incident light with a simple lens or a low power of the microscope the pigment presents a glittering metallic appearance, giving the surface a lustre like that of frosted silver. Viewed by transmitted light it appears dark and opaque. The pigment is scanty or absent in immature individuals.

**Integument and Muscular Layers.**—I have found no indication either in sections of specimens fixed by various reagents, or of macerated and teased specimens, of the division of the epidermal layer into cells.<sup>1</sup> Nuclei occur at irregular intervals; in diameter they average .004 mm. Externally the epidermis (fig. 3, *ep.*) in some series of sections appears bounded by a definite layer, which becomes more strongly affected by staining agents than the rest. This has been looked upon as a cuticle, but is regarded by von Graff as formed by the bases of the cilia. I do not think that it is

<sup>1</sup> In *Convoluta* von Graff (14) succeeded by maceration in isolating epidermal cells.

an independent layer, but that it is to be looked upon as a somewhat modified portion of the epidermis.

The cilia, which cover both surfaces, have an average length of about .008 mm. Here and there are longer flagella, which appear to be non-vibratile, but are often passively moved by the cilia at their bases. Each cilium consists of two segments, a proximal, straighter and stiffer, and a distal, more flexible and whip-like. Vertical lines in the protoplasm of the epidermis have the appearance of continuations of the cilia inwards.

In *A. cinereus* von Graff (15, p. 4) describes the epidermal cells as resting on the underlying muscular layer by a base which is often branched, the presence of the branches with the spaces between them giving an alveolar appearance to the inner zone. This appearance was not observed in *Heterochærus*.

In the case of *A. cinereus* von Graff states that, in addition to the true epidermal cells, and the gland cells with their ducts, the epidermal layer also comprises a number of cells which he terms interstitial cells. In *Heterochærus* these do not occur, at least in the same form; but stellate pigment cells (fig. 4) extending over the dorsal surface in mature specimens, and often spreading to some extent over the ventral, may represent them. The processes of these stellate cells are usually completely united into a network, and in most parts, at least in mature specimens, their cellular nature becomes obscured, especially since nuclei are very difficult of detection among the dense pigment, and it is, besides, very hard to distinguish them with certainty from the ordinary nuclei of the epidermis. In some cases, however, more particularly in immature specimens, it becomes manifest that the pigment is contained in stellate cells, the processes of which anastomose to form a network, extending through the epidermal layer towards its deeper surface.

Though the occurrence of epidermal pigment appears to be somewhat exceptional in the Turbellaria, yet bodies of the same nature as those here regarded by me as stellate pigment

cells combining to form a network, occur in other *Accela*. Von Graff, who re-directs attention to these in a recently published work (17) on the *Turbellaria* as parasites and hosts, does not express any definite opinion as to their nature, though he rejects his previous supposition that they might have some connection with the so-called "crystalloids" (really spores of a Sporozoan) occurring in certain fresh-water *Rhabdocœles*. But the regular distribution of the bodies in question, to form a bilaterally symmetrical pattern, and their restriction, or virtual restriction, to the dorsal surface, seem, with the other points already referred to, to render it evident that we have here to do with a normal constituent of the epidermal layer, and one which may be best regarded as a peculiar variety of pigment cell.

Here and there a little process or papilla projects on the surface of the epidermis; each of these is a mass of rhabdites projecting through an aperture in the epidermal layer—the opening of the duct of a rhabdite-forming gland. The rhabdites (fig. 5) are of two kinds,—shorter, fusiform, and longer, very slender. They often collect in packets in the ducts near their extremities. The ducts are sometimes longer, sometimes shorter—the glands being sometimes near the surface, sometimes more deeply sunk. When the rhabdites are discharged a sticky gelatinous fluid is poured out with them, and by means of this secretion the animal is able to adhere with surprising firmness to a smooth surface, quite a strong jet of water being necessary in order to displace it. In this the whole ventral surface shares; but the posterior processes maintain their hold most tenaciously. Rhabdites are given off freely on the dorsal as well as on the ventral surface. When there is some irritant present in the water, a rapid discharge takes place, and the animal becomes enclosed in a whitish covering, which soon stiffens to form a protecting cocoon. This is, in all probability, the main function performed by these integumentary glands. But it is quite likely that the secretion may have some effect in entangling, and

perhaps poisoning, the relatively large and often active animals on which this Turbellarian preys.

The muscular layers present no features calling for special remark. As in all the *Accela* hitherto described, there are three layers—an outer circular, a middle diagonal,<sup>1</sup> and an inner longitudinal. In addition, there is an abundantly-developed system of parenchyma-muscle, chiefly composed of dorso-ventral fibres.

The Algæ.—The symbiotic Algæ, in the full-grown animal, form two dense strata—one dorsal, the other ventral—just within the muscular layers. But they are by no means confined to these situations, occurring, often in abundance, all through the cortical parenchyma, and between the cells of the ovaries and the lobes of the testes. They also occur, though rarely, in the digestive parenchyma (fig. 7). In the smallest specimens, just escaped from the egg, only one or two of the Algæ are to be found; but they appear to multiply rapidly by fission, as somewhat larger specimens of the worm contain large numbers. They are, apparently, simply embedded in the parenchyma, and are not contained in the interior of cells. Sometimes they are isolated, more commonly they adhere together in irregular strings; but in the latter case the adhesion is very slight, and, when the host is crushed or broken up, the algal cells become detached from one another.

The Algæ (fig. 6) have an average diameter of .025 mm. They have a very definite shape—oval, with the broader end rounded and entire, and the other end usually with a distinct incision or notch, which may be double.

An important feature distinguishing this Algæ from that which occurs in *Convoluta*<sup>2</sup> is the presence of a distinct, though somewhat thin, non-protoplasmic cell-wall. This becomes very clear in stained cells, particularly when plasmolysed. It does not respond to the iodine and sulphuric acid

<sup>1</sup> In the figures of sections these diagonal fibres are not represented as distinct from the circular.

<sup>2</sup> Haberlandt (in 15), Gamble and Keeble (8).

test; but there can be little doubt, from its appearance and behaviour in other respects, that it is composed of cellulose.

The colour of the chromatophore, which occupies a large part of the interior, is somewhat variable. It is rarely grass-green, but always contains a brownish ingredient, and in some cases would be best described as brown with a tinge of green—the appearance presented closely resembling that of the chromatophores of Diatoms or Dinoflagellates. All the colouring matter is soluble in alcohol.

The nucleus always occupies the same position, in a mass of uncoloured protoplasm at the broader end of the cell. It contains a very regular chromatin network without nucleoli or other similar bodies. Towards the middle of the cell is a single spherical pyrenoid, very rarely a couple.

A large proportion of the *Acœla* seem to lodge “symbiotic” Algæ. In many cases these are bright green in colour, containing no other colouring matter than chlorophyll. But in *Haplodiscus*, and in some species of *Convoluta* and *Amphichærus*, they are yellow or brown. Whether the presence of a cell-wall is a special feature of the *Zooxanthella* of the Australian form remains to be determined.

In the case of *Convoluta*, Gamble and Keeble (8) conclude that the green cells are not of paramount importance in the nutrition of the worm, which freely ingests various organisms. In the Australian form there is still less need for any symbiotic nutrition, since recently-captured specimens are almost invariably found to contain relatively large animals—Rotifers, Polychæts, Crustacea, etc., in process of digestion.

Further details with regard to these Algæ are reserved for the present until more complete data have been obtained.

Digestive System and Parenchyma.—As in most *Acœla*, a pharynx is absent. To apply the term, as von Graff, Pereyaslawzewa (22), and others do, to what is neither more nor less than an integumentary pit with the epidermal layer somewhat thickened, appears to me to be misleading.



In *Heterochærus*, as will be rendered clear by fig. 8, representing a section passing through the mouth, the latter is an opening leading directly inwards—the integument and muscular layers being involuted round its margin to a very slight extent to form a very short passage, but not becoming modified in any way, except that the integumentary glands are slightly more numerous.

There is no intestinal epithelium—the food being received into a mass of nucleated protoplasmic material, which is devoid of definite arrangement, and is not distinguishable into cells. This is fibrillated, and consists of strands which have for the most part a radial arrangement, with irregular vacuoles between them. In sections of specimens in which no food is present the appearance represented in figs. 9—11 is fairly constant. There is always a relatively large, well-defined space (*ent.*) situated towards the middle, and representing the intestinal lumen. The mouth usually, as in the specimen represented in fig. 9, leads directly into the central space, but sometimes a mass of the plasmodium intervenes.

Surrounding this central space in a fairly regular manner are a number of smaller spaces, usually narrow and elongated, and having a general radiating arrangement. The partitions between these are composed of the same material as that surrounding the central space, but reinforced by a good many muscular fibres.

An extension of the central parenchyma in the form of a vacuolated horizontal plate runs out to the marginal region of the body on each side, and also forwards and backwards, and passes distally into the superficial layer. It is perforated by numerous dorso-ventral muscular fibres. Both above and below it is a series of vertically elongated spaces, like the cells of a honeycomb, with thin perforated walls. The substance of which the partitions are composed is of a more hyaline appearance than the central plasmodium, and is not fibrillated. Running in the partitions, but never through the spaces, are many dorso-ventral muscular fibres. The partitions end in the superficial layer of parenchyma. The

result of this arrangement of the parenchyma and its vacuoles is that in a transverse section the region between the central or digestive parenchyma and the superficial layer appears divided by numerous vertical lines, while in a horizontal section it has, more or less, the appearance of a cross-section of a honeycomb. This appears in figs. 9 and 10.

In the genital region, which occupies the greater part of the length of the body, the cells of the testis of each side lie in the series of spaces to the dorsal side of the horizontal plate, while the ovarian cells occupy the corresponding spaces on the ventral side, the plate thus acting as a partition between the two. The latter must act also as the main support for the digestive plasmodium.

Immediately within the body-wall the parenchyma forms a superficial layer, embedded in which are the greater number of the Algæ and all the rhabdite-forming glands, and in which lie also the main nerve-cords and the plexuses to which they give rise.

The whole structure and arrangement of the parenchyma in *Heterochærus* closely resemble those of that tissue in *Haplodiscus ussowii*, as described by Sabussow (24), particularly with regard to the horizontal plate and the sets of spaces above and below it.

The food consists of a variety of organisms, many of them comparatively high in the scale—Rotifers, small Polychæts, Entomostraca, small Amphipoda, etc. These are found in the large central space, or, if of minute dimensions, may be contained in the interior of the smaller vacuoles.

In the case of *Amphichærus cinereus* von Graff (15, p. 15, Taf. I, fig. 12) describes and figures special cells which he looks upon as concerned in the formation of a digestive secretion. In the case of *Heterochærus* the only elements at all resembling in appearance and position those represented are deep-lying Algæ; and nothing of the nature of special secretory cells is to be found.

From the above account of the digestive system of *Heterochærus* it follows that, in this form at least, the

subordinal name of *Acœla* is not strictly applicable, since an enteric cavity, of a sort, is undoubtedly present, and though liable to modification, fairly constant in form and position. To the alternative name proposed by Mdle. Pereyaslawzewa, viz. *Pseudo-acœla*, there is the objection, which appears to me formidable, that its proposal was founded on the erroneous conception that the apparent absence of an epithelium is due to the action of reagents. Perhaps the term *Adelocœla* might be adopted, if the conditions obtaining in *Heterochærus* should prove, on further investigation, to prevail in the other members of the group.

**Nervous System.**—There are three pairs of longitudinal nerve trunks—two dorsal, viz. inner and outer, and one lateral. The last are much the largest and most important. They extend throughout the length of the body, near the lateral margins, and nearer the ventral than the dorsal surface. From these main lateral trunks branches are given off, some of which break up to form a plexus in the shape of a network (fig. 13), extending over the entire ventral surface below the muscular layers. Anteriorly the two lateral trunks converge, and, about midway between the dorsal and ventral surfaces, enter the brain.

The two dorsal pairs of nerve-trunks unite to form, on each side, a common root, which is little more than a dorsally-directed process from the brain.

The brain (figs. 12 and 14) is a commissure of finely-fibrillated material which, on its upper (dorsal) aspect, gives off the roots of the dorsal trunks, while on a lower plane the lateral trunks pass out from it. Between the roots of the latter is a rounded median recess, open posteriorly, in the brain substance. This is partly covered over dorsally by brain substance, but is not so bounded either ventrally or posteriorly: it is almost completely filled by the otocyst (*ot.*). At the sides are the two small and simple eyes (*e.*), consisting merely of masses of pigment embedded in the substance of the ventral portion of the brain, which, owing to the presence of the otocyst recess, is divided into two lobes, each giving

off the corresponding lateral nerve. Nerve-cells surround the fibrillated material of the brain, and are most abundant over the dorsal portion.

The dorsal nerve trunks, four or, more rarely, six in number, run backwards beneath the muscular layers, and give off numerous branches, which branch and anastomose to form a plexus extending over the entire dorsal surface.

From the same part of the brain (the ventral portion) which gives origin to the lateral nerves are given off several nerves, which run forwards in the region in front of the brain, breaking up into numerous branches, forming a rich plexus, which extends to the anterior extremity.

Von Graff (15, p. 31) describes the brain of *A. cinereus*, but did not succeed in making out the arrangement of the longitudinal nerve-cords. The brain is, in its upper part, a transversely-elongated four-sided mass, bearing anteriorly two swellings, from which arise two nerves that unite to form the "anterior commissure." Below the brain increases in bulk, mainly owing to the accumulation of nerve-cells at its posterior angles giving rise to the dilatations from which the longitudinal nerves are given off, and to the presence of a pair of lateral swellings from which the "posterior roots" of the middle longitudinal nerves arise dorsally. The arrangement of the longitudinal nerves is supposed to correspond to that observable in *C. roscoffensis* as described originally by Delage (5). In this form there are six longitudinal nerves, which run parallel with one another to the posterior extremity of the body, where they lose themselves in a network of anastomoses. Delage terms these inner, middle, and outer pairs of longitudinal nerves. The last lie almost at equal distances from the dorsal and the ventral surfaces, while the other two are distinctly dorsal, lying immediately below the stratum of *Zoochlorellæ*. The two inner arise from the posterior angles of the more dorsally-situated part of the brain, while the others originate on either side from a common root which arises from the anterior (ventral) part. In addition the middle longitudinal nerve is connected with

the dorsal (posterior) ganglia of the brain by a transverse anastomosis going off from the outer angle, so that it has a double origin. Neighbouring longitudinal nerves are connected together by anastomoses between their branches, the arrangement of which is subject to variation in different individuals.

On the whole there is a very close correspondence between the nervous system of *Heterochærus* and that of allied forms. Owing to the absence of a frontal organ it is not possible to distinguish the "anterior and posterior commissures" described by v. Graff, and there is thus an appearance of greater simplicity in the brain. All the nerve cords, except the lateral and those giving rise to the frontal plexus, arise from the dorsal part of the brain, and this appears also to be a distinguishing feature.

The two little masses of pigment which represent eyes in the *Acœla*, instead of being situated in the epidermis as they are stated to be in other members of the group, are embedded in the substance of the brain. In this point *Heterochærus* resembles *C. schultzei* (Delage, 5, p. 131).

Reproductive Apparatus.—The male reproductive apparatus of *Heterochærus* does not differ in any essential respects from that of allied forms. The testes (fig. 2, *t.*) are composed of numerous minute lobes, which extend throughout the greater part of the length of the body towards its dorsal aspect. The two vasa deferentia have no definite walls, but are merely of the nature of channels in the parenchyma, which run backwards some little distance from the lateral margins, increasing in width as they receive additional accessions of spermatozoa from the testicular lobes. At its posterior end each vas deferens expands into a wide vesicula seminalis (*v.*), and these bend inwards to meet in a median reservoir at the base of the penis. Into this open the ducts of numerous unicellular glands, the secretion of which consists of, or contains, minute rounded granules. These glands appear to correspond to the prostate- or granule-glands of other Turbellarians. From the median reservoir a very short

and wide ejaculatory duct leads to the male aperture at the extremity of the penis. The penis is devoid of any chitinous parts. It is in the form of a truncated cone with muscular walls and an epithelium of cylindrical cells.

There are two very distinct kinds of spermatozoa—a larger and a smaller. The larger, or “giant” form (fig. 15) is .35 mm. in length—about eight or ten times the length of the smaller. It is a long, cylindrical filament. Of this the posterior portion, which tapers very finely, represents the tail, the greater part of the filament representing the middle-piece. Along the length of the middle-piece and tail runs a very inconspicuous, contractile, spiral flange. The head is represented by the anterior portion of the filament, which is not modified in any marked way, but is distinguishable from the middle-piece merely by being usually bent at an acute angle on the latter, and by being devoid of the spiral flange. No chromatin elements were brought into view in any part by the action of methylene-blue or gentian, unless two rows of minute granules which run throughout the length of the middle-piece are of this nature.

The smaller sperm (fig. 14) has likewise no definite head, but the anterior end is slightly enlarged, and terminates in an abrupt, nearly transverse, face. Some distance behind this the sperm becomes distinctly compressed, and this compression is continued to near the posterior extremity, where a short, uncompressed, filamentous portion represents the tail. Staining with gentian-violet brings out a series of granules in the axis of the middle-piece increasing in bulk towards its posterior end. The smaller sperm moves actively with a wriggling motion, during which it is thrown into a spiral. The movement is intermittent, and, when it ceases, the sperm usually becomes straightened out, but sometimes assumes various definite curves. The giant sperm moves with a gliding motion when a number are in contact, unless they are wedged very close. But it also sometimes executes wriggling movements of the tail part, which are much less active than those of the smaller sperm.

In connection with the subject of the spermatozoa it may be worth while to mention that a remarkable micro-organism, presumably a Schizomycete, which is extremely common as a parasite of *Heterochærus*, particularly in the winter and spring, bears a very considerable resemblance to a spermatozoon both in form and movements. It occurs in the interior of vesicles which are apparently degenerating cells, sometimes in the interior of degenerating Algæ, proved to be such by vestiges of the chromatophore. They are filaments thickened at one end, and they execute wriggling movements. Each vesicle or cell may contain only one or several of these bodies. They are only about .025 mm. in length, or a good deal smaller than the smaller sperms. They are doubtless similar in character to the "parasitische Gebilde," referred to by Böhmig (2)<sup>1</sup> and Sabussow (24, p. 377), and supposed by Monticelli to be spermatozoa.

The female reproductive aperture leads into a thick-walled passage (figs. 2 and 17, *ant.*), which may be termed the *antrum femininum*. This is lined with columnar ciliated epithelium, outside of which is a thick muscular coat, composed of external circular and internal longitudinal layers. Perforating the wall and opening into the lumen of the antrum are the ducts of a great number of unicellular glands (*gl.*), which produce a secretion precisely similar in appearance to that of the granule-glands of the male apparatus. The ducts are dilated just before they open to form reservoirs for the secretion, so that a great quantity can be discharged very rapidly. When they are discharged the granules become disintegrated, and give rise to a nearly homogeneous mass with irregular granulations.

From the antrum proper a passage runs upwards and forwards, and its upper extremity lies immediately below the integument of the dorsal surface. During the breeding season, but not at other times, the dorsal wall of the body in

<sup>1</sup> I only know this paper through abstracts in the 'Zool. Jahresbericht' and 'Zool. Centralblatt.'

this position always presents a colourless spot, owing to the absence, in the area directly over the antrum and female aperture, of the parasitic Algæ, and also of pigment. The area is always depressed, and in it there is frequently to be recognised an appearance like that of a closed cleft or fissure. In only a few cases was an actual opening observed. But the study of sections through this region shows that there is always, in sexually mature animals, an actual or potential passage, leading from the dorsal surface into the antrum. This appears most distinctly in sagittal sections, such as those represented in figs. 21 and 22, which are accurate copies of photographs. In all series of sections of specimens with ripe ova this cleft or passage is to be detected. This observation must have an important bearing on the question of the functions of the various parts of the reproductive apparatus, and will be referred to later. In the meantime I will point out that this passage, if not homologous, is at least closely comparable with the "canal of Laurer" of Trematodes.

Near its dorsal extremity the antrum, or, more correctly, the passage which continues it forwards and dorsad, gives off, nearly at right angles, the two ducts of the bursæ. These are lined externally with a continuation of the muscular layer of the antrum; but they have no regular epithelium, containing instead a somewhat irregular layer of cells, which does not bound a definite lumen, but has running through it several narrow passages. Those passages, and the lumen of the vagina, often appear blocked with the secretion of the unicellular glands.

Each of the lateral ducts into which the antrum divides terminates in the corresponding bursa seminalis (*b. s.*). The wall of this is composed of the same kind of material as the wall of the duct—a thin layer of muscle (fig. 18, *b. s.*) surrounding a mass of cells in which the remaining parts of the bursa are enclosed. Outside this is a thin layer of cells, the nuclei of which resemble those of the unicellular glands that surround the antrum. The bursa encloses the chitinous



mouth-pieces and a series of rounded bodies, which I will term bulbs, with one of which each of the chitinous pieces is connected.

From the irregular channels into which the lumen of the duct is divided a narrow canal (fig. 17, *d.*) runs to the base of each bulb, and, passing through it, enters the corresponding mouth-piece, through the axis of which it is continued to the free extremity. The canal is dilated (*d.*) immediately below the base of the mouth-piece, and sometimes, though rarely, there is a second dilatation further back.

The structure of the bulb (fig. 18) is exceedingly difficult of determination, owing to its being nearly always packed full of sperms. In the few cases in which this was found not to be the case, it had a shrivelled appearance. It must have a bounding wall preventing the escape of the sperms and maintaining its regular form, and internally it appears to be of the nature of a sponge. Mark's view that it is formed of greatly vacuolated and fused cells seems to me to be highly probable. The chitinous mouth-piece is attached to it by a number of fibres, which run from the basal part of the mouth-piece into the substance of the bulb. The spaces in the bulb must communicate freely with the canal as it passes through, to enable the sperms to be received, and to be afterwards discharged.

The chitinous mouth-pieces (fig. 18, *ch.*) are, on the whole, very similar to those of *Amphichærus* and *Polychærus*, as described by von Graff and Mark. Each is a slender cylindrical rod, tapering towards the extremity, and more or less strongly curved. Its chitinous wall consists of a large number of minute pieces (figs. 19 and 20), which are not rings, or perforated discs, as they are stated by von Graff to be in the species which he examined, but form each a little less than half a ring.

As the mouth-piece tapers towards its free extremity the chitinous segments undergo a corresponding reduction in size. Besides being enclosed by these chitinous bodies the fine canal has a wall of its own, and at the free extremity

this usually extends some distance beyond the last of the chitinous bodies.

From its base, which is slightly embedded in the bulb, to its apex the mouth-piece is enclosed in a sheath of cells (fig. 18, *ch. c.*) which are continuous with those of the wall of the bursa, and not widely different from them in appearance. These are arranged in a single layer with their long axes at right angles to that of the mouth-piece, and each is produced into a narrow lamellar process, which becomes connected with one of the chitinous bodies. These cells have nuclei similar to the nuclei of the wall of the bursa, situated towards their outer ends, but, in the fresh condition, these are barely visible without the addition of acetic acid.

In each cell, however, nearly always on the inner side of the nucleus, is, in most specimens, a rounded globule which, on account of its high refractive power, is very much brighter and more conspicuous than the nucleus itself. Like the cells themselves these globules gradually diminish in size towards the fine extremity of the mouth-piece. Each of them is of about the same volume as one of the chitinous bodies in its vicinity. It seems to me that these appearances point to the conclusion that the cellular sheath of the mouth-piece is composed of cells by whose action the chitinous matter is formed, and that the globules occurring in the interior of the cells are actually chitinous pieces in process of formation.

Where the canal enters the bulb from the base of the mouth-piece it becomes dilated, as already mentioned, into a rounded cavity (fig. 17, *d'*) in the substance of the bulb.<sup>1</sup> In the interior of this are a number of crescent-shaped bodies, .008 mm. in length, narrower at one end than at the other, apparently composed of the same material as the parts of the mouth-piece. In sections these appear irregularly arranged, but in their natural relations they are, in all probability, disposed in a regular way around the lumen with their concavities in-

<sup>1</sup> In some specimens a second enlargement, presenting very similar appearances, occurs further back.

wards, like the bodies in the wall of the mouth-piece itself. It is these crescent-shaped bodies, I apprehend, that are referred to by von Graff (15) as gland-cells, and that are also noticed by Mark (20) in *Polychærus*. One end of each of these, the broader, becomes much more strongly stained than the rest, and this appearance may have led to the supposition that the bodies in question are of the nature of cells. The narrower end is continuous with a fibre or fibres, which pass outwards into the substance of the bulb. It seems to me that the presence of these chitinous bodies in the interior of the bulb, with the fibre-like strands passing out from them, points directly to the conclusion that the bulb is composed of cells which, originally, like those forming the investment of the mouth-piece, have lost, for the most part, their secreting power, and have coalesced and become vacuolated to receive the sperms.

The free extremities of the mouth-pieces extend far beyond the wall of the bursa. Towards the extreme point, where the chitinous bodies become discontinued, the slender canal loses all traces of sheath, and terminates in the parenchyma, near the ventral surface of the body, in close proximity to the posterior extremity of the ovary and the ripe ova. In several specimens I was able to see sperms issuing from the end of the canal, and wandering out into the surrounding parenchyma.

In number and arrangement the chitinous mouth-pieces are very irregular. Most commonly there are four in each bursa; but in some cases there were only two, and in others as many as nine. Very often the number in the two bursæ is unequal. In one specimen the entire bursa was duplicated on one side, though not on the other. Often a bulb, or more than one, has no mouth-piece. Nearly always two of the bulbs are partially fused. Very frequently one or more of the mouth-pieces are incomplete—the basal part, usually, being absent,—as if in course of absorption or regeneration.

The parts just described, namely, those known as bursæ seminales, with their chitinous mouth-pieces, are very im-

perfectly understood; and various conflicting statements have been put forward as to their structure and functions.

The account of them given by von Graff (15), in the case of *A. cinereus*, is assuredly incorrect, unless that species differs in a very thorough and radical manner from the Australian form. He represents the female genital aperture as leading into a sort of vestibule, from which, in turn, lead three passages—a median and two lateral. The former is a short and wide passage leading backwards into a cavity—the cavity of the bursa seminalis,—which becomes filled with a mass of spermatozoa as the result of an act of copulation. The two lateral passages are much narrower than the median; they curve outwards and backwards and open into the bursa seminalis. In the posterior part of each of them is lodged the corresponding chitinous end-piece, the base of which is supported on the mass of spermatozoa, while the apex is directed towards the external opening. Each mouth-piece is described as a curved, tapering rod, made up of a series of perforated chitinous discs, the central canal being bounded by a longitudinally striated *membrana intima*. Surrounding the chitinous tube is a layer of ring-shaped cells, each of which is the matrix cell, or formative cell, of one of the chitinous discs.

Von Graff regards the mouth-pieces as organs capable of eversion, and of acting as organs, by means of which spermatozoa are transferred to another individual, the lateral passages, with their chitinous mouth-pieces, being regarded by him as the parts by means of which the ova are fertilised when discharged. But in *Amphichærus* and *Polychærus*, as in *Convoluta*, it has been shown by Pereslawzewa (21), Rapiachoff (23), Mark (20), Gardiner (10), and others, that the eggs are internally fertilised.

A deeper insight into the structure and mode of action of these organs was attained by Mark (20), who studied them in his *Polychærus caudatus*, in which there are a number of mouth-pieces on each side, instead of merely one as is usually the case in *A. cinereus*. "Each chitinous structure consists

of a slightly tapering, conical, central portion, which is traversed by a narrow axial canal, and from which diverge numerous thin, close-set lamellæ, which are directed obliquely outward and towards the narrower end of the central piece. . . . From the arrangement of the nuclei at the periphery of the ventral portion of each such organ, I conclude that the chitinous structures result from the secretion activity of cells whose nuclei occupy their peripheral ends, while the axial blade-like prolongations of the cells extend as far as the conical chitinous axis, and separate the successive chitinous lamellæ which go off from the latter. The basal end of the mouth-piece is surrounded by enlargements, which are probably identical with the "Drusenkranz" figured by von Graff (Taf. II, figs. 1 and 2) for *Amphichærus*. . . . Cross-sections of the chitinous mouth-pieces and their surrounding mantle of cells show that both are circular, and that the lumen of the former is likewise cylindrical and very narrow. Lying in a vacuole near the basal or larger end of the chitinous cone—sometimes in contact with it—there is almost invariably a small ball of tangled spermatozoa. . . . The exact histological nature of the deep or dorsal half of these cell-masses—the ventral portions of which secrete the chitinous mouth-pieces—is not easily determined. The substance of adjacent masses seems to be more or less confluent into a finely granular pale substance, in which are scattered a few faintly coloured nuclei. The appearance is as though the cells of the deep half of each cluster had become distended into enormous gland cells, and then, becoming confluent with each other, had finally become vacuolated, and lost to a great extent their cell boundaries. . . . There are small lacunar passages, in the parenchyma between the ventral ends of the ovoid masses and the ventral wall of the body, and I imagine that these serve in some way to transmit the spermatozoa to the ova, but I have not yet found spermatozoa in these passages nor even satisfactory evidence that they pass through the narrow lumen of the chitinous mouth-pieces" (pp. 307 and 308).

Gardiner (10) states that he has frequently seen one specimen of *Polychærus caudatus* pursuing and trying to get on the back of another, which showed symptoms of restlessness and discomfort, and endeavoured to escape. Under the dorsal integument of the second individual, in such a case, were found numerous spermatozoa, and in the vicinity abrasions were observed. From these facts he concludes that we have here an example of hypodermic impregnation, and that the function of the chitinous mouth-pieces is to bring about this result.

This appears to me not to be a tenable view of the function of the parts. There is no direct evidence that the bursæ are capable of being everted in such a way as to be brought into play as organs for effecting hypodermic impregnation, and it appears very improbable, from their structure, that they are capable of being so used. Moreover, such a theory involves a supposition which bears great improbability on its face. We should have to suppose that in these animals we have a process of fertilisation without parallel in the animal kingdom—a process in which one individual, having received into a part of its female apparatus a mass of spermatozoa from another, uses them to impregnate a third!

The conclusions to which I have come with regard to the functions of these parts have already been partly indicated. The observation of the passage of a stream of spermatozoa from the apex of the mouth-pieces into the tissues in the near neighbourhood of the mature ova (previously also recorded by Repiachoff [23] with reference to another member of the group) seems to prove the function of the bursæ to be the internal fertilisation, one by one, of the ova as they become mature. The structure of the parts seems to render it unlikely that the spermatozoa so utilised can be derived from the same individual, so that a process of copulation, though not actually observed, most probably occurs. This may take place, not through the ventral female aperture, but through the dorsal passage (Laurer's canal) the existence of which is otherwise not easy of explanation, and, if so,

in all probability, the eggs pass out through the antrum femininum.

Like the testes the ovaries (fig. 2, *ov.*) are devoid of any investment. Each simply consists of a number of cells which extend on a more ventrally-situated plane than that on which the testes lie, from near the anterior end of the body to the neighbourhood of the oviducts. There is no differentiation of vitellogen cells or shell-gland cells. The most anteriorly-placed cells are the smallest, and their size gradually increases as we pass backwards until we reach the ripe ova. The nuclei of all the unmaturing cells are of the same character. In the larger ova they are .05 mm. in diameter. There is a loose chromatin network and a large nucleolus, .02 mm. in diameter, within which are to be detected either one or two spherical bodies, having the appearance of vacuoles. The protoplasm of the ripe ova is very mobile, and, if it does not undergo active amœboid movements, readily flows backwards and forwards through the spaces in the parenchyma in which the ovaries are situated. Usually the full-grown ova are drawn out in the direction of the long axis of the body and they may attain a length of .4 mm.

In the posterior part of their extent the two ovaries become more or less completely united behind the digestive cavity, and in this position during the breeding season are to be found a varying number (sometimes as many as eighteen) of completed and fertilised eggs. These (fig. 2, *oo*) are usually subspherical. With few exceptions all the many eggs examined were in precisely the same stage, viz. that of the first segmentation spindle. It would appear, therefore, that at this stage there is an arrest in the development, and that the process only goes on further when the egg is discharged.

Maturation-stages were very rarely met with—a circumstance that would seem to point to the conclusion that the process takes place very rapidly. In the stage immediately following, the female pronucleus (fig. 24) has the peculiar character described and figured by Gardiner in *Polychærus*,

having the appearance of a rounded group of vesicles each enclosing a minute spherical mass of chromatin. This appearance it still retains after the sperm has entered the cytoplasm, the actual union of the male and female nuclei was not observed. The polar bodies (fig. 23, *pl.*) were embedded in the cytoplasm not far from the surface in all cases in which they were detected, and if they ever become actually separated out, the separation evidently takes place at a later stage.

The material of the thin egg-shells in which the fertilised ova are enclosed is secreted by the ova themselves, and not derived from any special glands. In some eosinated preparations this is rendered very obvious, some of the ova being surrounded by a discontinuous investment of droplets or granules, others having a complete shell, while droplets or granules of what appears to be the same material are discernible in the substance of the ova, both fertilised and unfertilised, and in the spaces between them.

The mode of passage of the fertilised eggs to the exterior remains doubtful. The spaces in which they lie have no definite outlet. Gardiner gives a diagram of the parts in *Polychærus* in which the "vitelline glands" enclosing the eggs are represented as opening on the exterior by means of the female aperture. This is not in accord with Mark's observations on that genus. In *Heterochærus* such a communication does not exist. I can merely conjecture that when a number of completed eggs have accumulated a temporary passage is formed between the space in which they lie, and the lumen of the antrum. A short, blind, anterior diverticulum of the latter, which occurs in some specimens, and is shown in fig. 17 (*k*) may be a vestige of such a temporary outlet.<sup>1</sup>

During the breeding season, when a number of specimens were kept for a day or two, many of them deposited their

<sup>1</sup> Gamble and Keeble (8) state that in *Convoluta roscoffensis* the eggs may be laid singly without disintegration of the parent, or a number are discharged at once with rupture of the parent, which sometimes breaks into two parts.



eggs on the bottom of the vessel. I have never witnessed the act of oviposition, and it probably takes place during the night. Solitary eggs are occasionally found; but, as a rule, a varying number—sometimes as many as thirty—are found enclosed together in a transparent capsule adhering to the glass. The capsule is structureless with, frequently, included foreign bodies, such as unicellular Algæ. Often spermatozoa of the animal are embedded in it. The individuals from which those eggs were discharged were found not to be ruptured in any way, and there seems to me to be little doubt, that the eggs pass out through the female aperture, and that the substance of the capsule consists of the secretion of the unicellular glands opening into the antrum femininum.

A remarkable point is that the reproductive apparatus is entirely absent during the winter. In specimens collected in April it was found to be intact, and in many there were fertilised ova. In the latter symptoms of degeneration showed themselves, however, most containing large vacuoles in the cytoplasm, though the nuclear spindles were still intact. But in June, July, and August none of the specimens examined showed any trace of reproductive apertures, and the examination of sections of a number showed not only that the apertures were completely absent, but that there was no vestige of reproductive apparatus, either gonads or ducts. These were full-grown specimens, resembling in every other respect those found two months before to contain mature sexual organs. Whether this means that the reproductive system becomes completely absorbed in the winter, to be regenerated in the spring, or whether it is that the generation which was sexually mature in April had perished, and a new generation had become fully grown without showing any rudiments of the gonads or their ducts, still remains to be determined.

Part II. On *Anomalocœlus cæcus*, a new type of  
Rhabdocœle.

The Rhabdocœle Turbellarian, of which the following is a description, was found among the mud at the bottom of dams at Glanmire Hall, near Bathurst, in New South Wales. Its eyeless condition is, doubtless, correlated with the fact that it was never found on the surface, but always burrowing more or less deeply in the mud. Nothing is known of its range; it does not occur in any of the other dams in the neighbourhood that were examined for it, and has not been found elsewhere.

The largest specimens were about 5 mm. in length when alive and fully extended: the breadth under the same conditions was about one-sixth of the length. The living animal is semi-transparent, of a reddish colour, which varies greatly in intensity. The region in front of the pharynx is always bright red, the colour being usually most intense in an axial streak in front of the brain. In young living specimens the intestine is clearly distinguishable as a cylindrical, rather opaque, band behind the rounded pharynx: in older specimens this becomes hidden by the reproductive apparatus. The vitelline glands appear as a glistening network extending over the entire post-pharyngeal region. The mouth is a rounded aperture situated anteriorly about an eighth of the total length from the anterior extremity. There is a single reproductive aperture situated somewhat in front of the middle of the ventral surface.

Integument.—The most important feature of the integument is the presence of a system of canals between the epidermal cells. The epidermal cells are flat polyhedral plates, like those of the majority of Rhabdocœles. They vary greatly in size, but are on an average about .04 mm. in length and .012 mm. in thickness. Each contains a nucleus (about .005 mm. in diameter), which is very rarely spherical, but nearly always lobed or mulberry-like. The cell-proto-

plasm is vertically fibrillated. Each cell is perforated by the ducts of a number of rhabdite-forming glands. When these are empty they are clearly to be recognised in stained sections as perforations passing through the cell; when secretion has been passing through them at the time of fixation it becomes strongly stained, and the effect in horizontal sections is the appearance of a number of dark spots in the body of the cell, and in vertical sections of a number of narrow, vertical, deeply-stained strands passing right through the cell, and sometimes projecting slightly on the surface. A thin layer on the surface of each cell marked by innumerable fine vertical lines, corresponding apparently to the bases of the cilia, is probably of the nature of a cuticle, but it is not very sharply differentiated, and there are no indications that it is capable of being detached from the underlying layer. The epidermis is supported on a distinct, but thin, basement-membrane.

The system of channels above alluded to is not equally distinct in all specimens, owing to the channels being sometimes more, sometimes less, dilated. In a favourable specimen the entire dorsal surface, and, in some cases, the ventral also, of the living worm is covered with a network of clear bands of varying width. When the surface is examined under a moderately high power of the microscope, it is found that these bands lie in the intervals between the cells of the epidermis, and represent branching vessels of varying calibre. In one or two of the specimens which I fixed and mounted whole these vessels are almost as distinct as they were in the living condition. In fig. 29 I have represented a portion of this network as seen in a surface view of one of these entire preserved specimens. Examination of the living specimen showed clearly that the appearance in question is not due to the presence of open clefts between the epidermal cells. In an uninjured animal no such clefts exist, the ciliated surface being smoothly continued without interruption from one cell to another across the clear interval. But in the majority of my series of sections, in cases in which the system is well

developed a rupture has taken place, so that what were in the natural state, closed tubes, assume the character of open clefts between the cells. In many cases, however, the closed character is retained. Such sections as those represented in figs. 26 and 28, which are facsimile copies of photographs, show that we have to do with a system of fine vessels which run in the intervals between the cells of the epidermis. They are superficially placed, and, while their lateral walls are formed by the edges of the cells, their outer wall, formed, apparently, by an extension of the protoplasm of both the contiguous cells, with the "cuticle," is exceedingly thin, and is readily ruptured during the processes of fixing and sectioning. The deeper portions of the cells are united underneath the vessels by numerous fine protoplasmic filaments.

In several instances in living specimens I thought I was able to trace a connection between this network of capillaries<sup>1</sup> and small vessels of the excretory system, and it appears very likely that such a communication exists, and that the network is to be looked upon as an extension, perhaps respiratory, of the water-vascular system.<sup>2</sup> That this plexus should vary greatly in different individuals as regards the degree of distinctness with which it appears, accords well with the character of the excretory system in general, in which the vessels frequently collapse and vanish completely, and, when they are in a contracted state, are quite indistinguishable.

It is unlikely that the occurrence of this remarkable network of channels forming an inter-cellular plexus of capillaries in the epidermal layer is a peculiarity of *Anomalocœlus*. In fact, there seems to be some evidence, if only in certain of the figures of von Graff's 'Monograph,' that the same thing occurs in some other groups of Rhabdo-

<sup>1</sup> I use this term as a convenient one, though the varying calibre of the vessels in question renders it not strictly appropriate.

<sup>2</sup> The only reference which I have discovered to excretory vessels in the epidermal layer is Vejdovsky's statement (28, p. 183) that in *Bothrioplana* blind branches extend into that layer.

cœles. This, however, is a subject for further investigation. I will merely at present direct attention to the figures of the epidermis of *Mesostomum Ehrenbergii* (Taf. v, fig. 12), *M. tetragonum* (Taf. iv, fig. 19), and *M. lingua* (Taf. vi, fig. 1), *Microstomum lineare* (Taf. xv, fig. 4), and *Vortex viridis* (Taf. xii, figs. 4 and 5). As regards the last-named species, fig. 4 represents a vertical section in which there appear between the cells rounded spaces having very much the same appearance as those occurring in the case of *Anomalocœlus*; in the explanation, however, the author refers to them as "Bindegewebeslücke." In the general part of the text (p. 45) the author remarks on this figure:—"Dass auf dem Querschnitte (fig. 4, v) so grosse Hohlräume zwischen den einzelnen Zellen übrig bleiben, erkläre ich mir aus der durch die conservirende Flüssigkeit hervorgerufenen Schrumpfung, wodurch die Fortsätze benachbarter Zellen sich von einander zurückzogen."<sup>1</sup>

The only definite statement I have succeeded in finding concerning such a system of intercellular channels in the epidermis is a brief one by M. Braun (4, p. 35). In his account of *Mesostoma platycephalum* he has the following:—"Die Haut besteht aus grossen, platten, am Rande mit Zacken besetzten Zellen, deren freie Fläche etwas grösser ist als die Basis; der Querschnitt einer solchen Zelle erscheint dann trapezformig mit eingebogenen kurzen Seiten. In Folge dieser Gestalt sieht Man zwischen zwei Zellen immer einen rundlichen leeren Raum auf dem Schnitt, der den schon von Graff abgebildeten Gängen zwischen den Epithelzellen entspricht; falls das Ganze nicht auf Rechnung der Reagentien zu setzen ist, findet sich hier, wie bei vielen anderen Rhabdocœliden, ein System von Kanälen, welche

<sup>1</sup> In connection with this subject it may perhaps be as well to point out here that the "wasserklare Räume," to which particular attention has been given by Böhmig (2), are intra-cellular, and that, whatever be their significance, and that of the pore-canals that run inwards from them, they have nothing to do with the capillary network. The latter manifestly does not occur in the genera (of Rhabdocœles), in which Böhmig made a special study of the integument.

um die Epithelzellen verlaufen, nach aussen und seitlich von den letzteren, nach innen noch zum Theil vom Hautmuskelschlauch begrenzt werden." That these canals are not, as it is here suggested they may be, formed as the result of the action of reagents is rendered evident by their conspicuousness in living specimens. But even if we had not that evidence, their arrangement in such a preserved specimen as that from which fig. 29 was drawn, following as it does a regular system, appears to me to be quite convincing. In such a view as that represented, which is a small part of what extends over the entire surface, main channels are traceable, giving off branches, the size of which is, on the whole, very uniformly regulated by that of the vessels from which they are derived. To bring this about, cells of a variety of sizes and of innumerable shapes are fitted in together in a highly-complicated manner.

In Schneider's 'Lehrbuch der vergleichenden Histologie der Thiere' there is a figure (fig. 317) of the epidermis of *Planocera folium*, which is given, rather strangely, to illustrate the structure of *Dendrocœlum lacteum*. In this is shown an intercellular space, which is not unlike those we are considering, but is made to perforate the basement membrane. In the text the author says:

"Zwischen den Deckzellen finden sich oft deutlich hervortretende Interzellularlücken; auch wurden in den Zellen vieler Turbellarien (Sekera, Böhmig u. a.) helle aufsteigende Kanälchen beobachtet die einerseits die Grenzlamelle durchsetzen und mit dem Enchym zusammenschlingen andererseits auch nach aussen ausmünden können. Die Kanäle nehmen oft den character weiter vacuolen an. Sie sind wohl als Lymphkanälchen zu betrachten" (p. 296).

Here it is to be observed that it is the first clause of the first sentence only that refers to intercellular spaces. The rest deals with Sekera and Böhmig's "wasserklare Räume," which have never been shown to have anything to do with the intercellular spaces. The figure, unfortunately, seems to combine two quite distinct spaces—an intercellular space and

one of Böhmig's "Porenkanälchen"—which perforate the basement-membrane and the cells. The appearances represented, however, correspond neither to the Triclad Dendrocoelum nor to the Polyclad Planocera.

Digestive system.—The pharynx belongs to the type of von Graff's "pharynx rosulatus," which is characteristic of the Mesostomida and Proboscida. It is of rounded shape, its oral opening situated near the anterior end of its ventral wall, and its oesophageal near the posterior end of its dorsal wall. A thin, external, circular layer of muscular fibres lies outside the longitudinal layer. The latter consists of a single layer of broad flat fibres, whose edges are in close apposition. In the dorsal and ventral, but not the lateral, walls the radial muscles are arranged in regular rows. Between them are the gland cells, the secretion of these is very fluid, and, in the living specimens, is to be observed to run freely backwards and forwards in the spaces between the radial muscles. The internal circular layer of muscular fibres is much the thickest. The internal lining membrane has lost its epithelial character, and presents no trace of division into cells, though a nucleus occurs here and there at wide intervals. A number of unicellular glands lie around the junction of the pharynx with the intestine.

Retractor and protractor muscles pass from the pharynx through the parenchyma to the muscular layers of the body wall. One strong bundle passes straight forwards in the middle line from the anterior wall of the pharynx to the anterior extremity of the body, causing the brain to be slightly indented on its lower surface as it passes it. It is accompanied by red granular matter which renders the whole structure somewhat conspicuous in the living animal.

The intestine has an irregular space representing the lumen bounded by a mass of cells, which does not assume the character of an epithelium, and is not bounded externally by any muscular or fibrous layer. The enclosed cavity, though irregular in shape, must be fairly constant in position, since the dorso-ventral muscular fibres which traverse its wall in

great numbers, never pass through the cavity itself. This is very similar to the form of intestine characterising *Gyrator*, as described by Hallez (18, p. 568), and *Macrorhynchus*, *Acrorhynchus*, and other *Proboscida* according to von Graff (14, p. 94). A lumen is said to be absent in these in the adult condition, but by this is probably meant a definitely-bounded cavity.

Behind the intestine proper, between it and the posterior border, there was frequently to be observed in living specimens a space, the walls of which occasionally contracted; this was often observed to contain various foreign bodies, and, in some instances, living spermatozoa. A very slight pressure caused rupture and the discharge of the foreign bodies. In sections of some specimens this posterior diverticulum of the intestine is to be recognised as a space enclosing such objects as the setæ and other remnants of aquatic *Oligochaeta*. This is a feature which I have not observed in any other *Rhabdocœles*, and one which appears to be of considerable importance.

**Excretory System.**—The excretory system was not traced out with adequate thoroughness. It was not in every specimen that vessels were visible at all in the living state; when contracted they seemed absolutely to vanish. The absence of specialised walls which this seems to imply is also indicated by the fact that of the numerous specimens sectioned (fixed mainly by strong Flemming or by Lang's solution), there is not one in which it is possible to follow with certainty the course even of the largest vessels.<sup>1</sup>

There are two main longitudinal vessels on each side, running more or less parallel with one another, the one on the dorsal, the other on the ventral side of the vitelline glands. Of these, the more dorsally situated bifurcates anteriorly close to the anterior margin of the pharynx, one of the branches running transversely inwards just behind

<sup>1</sup> In all probability young specimens would prove very much more favourable for the study of the vessels than the adults; but hitherto none but fully-mature animals have been observed.



the brain to join the corresponding vessel from the opposite side, while the other runs forwards to join the anterior prolongation of the ventral vessel.

Posteriorly both vessels usually become wider. In some specimens they united behind some distance from the middle line, and there was no evidence of any approximation of the right and left vessels, so that there would appear to be two separate excretory apertures at or near the posterior extremity.

Both of these longitudinal vessels were sometimes observed to contract peristaltically, sometimes with an approach to regularity.

A small number of ciliary flames were observed in very close relation to the main vessels—so close in fact that they moved with the movements of the vessel in such a way that they actually seemed to lie in the interior of the cells, forming its wall, or to be contained in extremely short branches.

In view of the meagreness of the above statement, it would scarcely be profitable to institute a systematic comparison between the excretory system of *Anomalocœlus* and those of described genera of *Rhabdocœles*. Apparently, so far as the arrangement of the main trunks and their mode of opening is concerned, the nearest alliance is with the *Vorticida*. The statements of O. Schmidt (25), Hallez (18, p. 21), and von Graff lead to the conclusion that, whereas in *Vortex* the main vessels open in the neighbourhood of the pharynx, if not actually into the pharyngeal sac, in *Derostoma* they open on the exterior by two apertures situated towards the posterior extremity. More recently Fuhrmann (7) has stated that in this respect *Vortex* and *Derostoma* are alike—the apertures in both genera being situated far back.

Reproductive Apparatus.—The testis is diffuse, its lobes extending throughout the part of the body situated behind the pharynx. Definite ducts are not developed, but by some means the sperms filter through channels in the parenchyma to the vesicula seminalis, which is situated in the anterior part of the space enclosed by the penis sheath.

From this the median ejaculatory duct runs backwards to the penial opening. Laterally a pair of strands of granule (prostate) ducts pass within the penis sheath, and strings of granules accumulate on either side of the ejaculatory duct to form a granule reservoir. The unicellular granule or prostate glands are scattered through the surrounding region, extending outwards nearly as far as the lateral border, and nearly to the posterior end.

The muscular penis sheath encloses the vesicula seminalis, the ejaculatory duct, the granule reservoir, and the penis. Posteriorly it divides into two layers, one becoming continuous with the wall of the penis, the other with that of the genital atrium.

The penis is a wide tube with thin and flexible walls, armed with chitinous teeth. The entire inner surface is beset with these teeth, which, extremely minute in front, become of relatively large size towards the opening of the penis into the atrium. The largest teeth, .08 mm. in length, vary in number in different individuals from three or four to twelve or more. The teeth are situated on the inner surface of the eversible penis when at rest, with their apices directed inwards, and must bristle outwards when protrusion takes place. Between the penis sac and the enclosed structures is a space filled with some uncolourable substance, through which extends in sections an irregular felt-work of fine filaments. This becomes closer towards the line along which penis sheath passes into penis, and, notwithstanding their extreme fineness, these fibres are doubtless muscular. It is the contraction of the muscular sheath that, acting through the contained fluid, must be the means of causing the eversion of the penis. Annular fibres constitute a sphincter of the sheath. The ejaculatory duct, traversing the penis, opens into a cavity of small size with muscular walls, into which the oviduct and bursa copulatrix open; this is the genital atrium.

The single ovary lies close to the penis sheath, on its right side anteriorly. It is of compact elliptical form, with its long

axis directed obliquely outwards and backwards. It is covered with a thin investing layer containing a few widely sundered nuclei. Towards the inner end (base) one or more of these nuclei may be observed sunk below the level of the investing layer. The inner end of the ovary contains numerous nuclei intermediate in character between those of the investing layer and those of the more mature ova. That the cells of the investing layer actually become converted into ova in the mature animal there is not sufficient evidence to establish definitely.

With the exception of its inner end the ovary consists throughout of ova which extend right through the organ from side to side.

Close to the ovary, and somewhat posterior as well as external to it, is the receptaculum seminis. It has a wall composed of a small number of cells with homogeneous protoplasm, usually not clearly distinguishable from one another. Internally this wall gives off irregularly arranged processes, which, though not forming actual partitions, give the outer part of the cavity a cellular character. In the interior is always a mass of spermatozoa.

The oviduct, continuous with the receptaculum seminis, and opening towards the ovary, with the investment of which its outer layers are continuous, runs backwards, and then curves inwards to open into the atrium. Its muscular layers, thin in front, become greatly increased in thickness posteriorly. On the same side of the atrium as the oviduct (i. e. the right) opens a sac which appears, in position at least, to represent the bursa copulatrix. It is an oval sac, of small size, with thinnish wall, devoid of chitinous parts, which opens by a narrow neck or duct into the atrium.

The atrium does not open directly on the exterior, but leads into a rounded chamber which acts as a uterus, and from this the common genital aperture leads outwards. The uterus is thus, as in most Proboscida and others (von Graff, 14, p. 139), merely the outer part of the atrium. In the uterus an egg, fully or partly completed, was very frequently found. Into

the cavity of the uterus, and into that of the bursa copulatrix, open the ducts of numerous unicellular glands—the shell glands,—which lie all round this part of the reproductive apparatus, and reach nearly as far as the lateral margin of the body. When an egg is not present in the uterus, the latter contains a quantity of fibrillar matter, which is perhaps coagulated secretion from the shell glands. In one living specimen the bursa copulatrix was observed to contain a number of rounded yellow globules, somewhat smaller than the vitelline spherules. These perhaps consist of the secretion of the shell glands, of which this sac may perhaps act as a reservoir.

In many specimens an egg was found in the uterus. Its shell was always so thick and opaque as to prevent any satisfactory view of its contents being obtained, except in one instance in which the formation of the egg-shell was incomplete. Enclosed within the transparent egg-shell in this specimen was the unsegmented oosperm surrounded by a mass of yolk-corpuseles. The oosperm was  $\cdot 06$  mm. in diameter, the corpuseles, on an average, about  $\cdot 04$  mm.

The vitelline glands form a continuous network extending throughout all the post-pharyngeal region. In the cytoplasm of the cells two kinds of material are produced. One of these appears first as extremely fine spherical granules or droplets, which become stained with eosin. These become aggregated into larger masses. The other substance is not colourable; it forms larger irregular masses. These two sets of elements escape from the cell into the irregular lumen of the gland; there is no evidence that the cell itself breaks up to form a part of the vitelline substance, and no evidence of the active cell-multiplication which such a process would entail.<sup>1</sup>

Moreover, in the completed egg the very characteristic and readily-recognisable nuclei of the vitelline cells are not to be recognised.

<sup>1</sup> Von Graff (14) describes a breaking down of the vitelline cells in *Turbellaria* in general, and Hallez (18) speaks of a continuous multiplication by division.

The fully-formed egg is .25 mm. in greatest diameter. It is not spherical, but more nearly of the form of a hemisphere, with one side strongly convex and the other flat. It is enclosed in a hard, opaque, chitinous shell.

After being formed the egg does not appear to remain very long in the uterus, but soon drops out to lie among the mud. A good many were picked out of the sediment at the bottom of the vessel, and were treated with a solution recommended by Hemming for softening chitin, but I was disappointed to find that, though some of them had been kept in water for days after being laid, none of those of which successful sections were made had developed, each containing the unaltered oosperm (in one or two cases two) with its enclosing mass of vitelline matter.

Affinities.—The combination of characters with which *Anomalocœlus* presents us places it outside the limits of all the known families of the Rhabdocœla. The arrangement of the male ducts (with the vesicula seminalis and prostate-reservoir both enclosed in the penis-sheath) is a very exceptional one, occurring among previously-known forms only in the Vorticida, from all of which the new form is distinguished (1) by having diffuse or follicular testes, and (2) by having a pharynx rosulatus instead of a pharynx doliiformis.

The possession of follicular testes is also a somewhat exceptional character, occurring only in the Alloiocœla and in the genera *Mecynostomia* and *Alaurina*, with none of which *Anomalocœlus* has any close alliance in other respects.

Von Graff (14, p. 217) enumerates those genera in which the ovary is single. Of these *Prorhynchus*, *Microstoma*, and *Anoplodium* may be at once left out of account as widely differing from the new form in many respects. We may also rule out, as manifestly not nearly related, *Omalostoma*, with its pharynx simplex and two reproductive apertures, *Byrsophleps*, which has compact rounded testes and two reproductive apertures, *Mesostoma* and *Castrada*,

with their elongated compact testes, and Solenopharynx, with its compact testes and elongated tubular pharynx.

There remain the Vorticid genera *Vortex*, *Jensenia*, and *Derostoma*, and the Proboscidan genus *Gyrator*. Of the former group *Vortex* and *Jensenia* have a pharynx *doliiformis*, compact paired testes, and unbranched vitelline glands, while *Derostoma*, though it also has compact testes, has the vitelline glands reticulate, and has sometimes a pharynx *variabilis*, while, like the other Vorticid genera, as mentioned above, it resembles *Anomalocœlus* in the special arrangement of the male ducts. *Gyrator*, even if we were to regard the strand of fibres in front of the brain in *Anomalocœlus* as a rudiment or vestige of a proboscis, is pretty widely removed, owing to the possession of compact testes and two reproductive apertures; and of the other Proboscida, *Pseudorhynchus*, which is perhaps the nearest, has two ovaries and compact testes.

On the whole, perhaps the closest affinities of *Anomalocœlus* are with some of the Vorticida; but these affinities are not sufficiently close to allow of the new genus being included in that group. Thus, if we follow the general scheme of division adopted by von Graff, it will be necessary to form a new family for the reception of this genus. Following von Graff's phraseology, we should define the family *Anomalocœlidæ* in the following terms:—*Rhabdocœla* with one reproductive aperture, a single ovary, the uterus combined with the genital atrium, reticulate vitelline glands, diffuse testes; with the vesicula seminalis and prostate reservoir enclosed in the penis-sheath; the penis armed with numerous chitinous teeth; the pharynx a pharynx *rosulatus*; the intestine devoid of a definite layer of epithelium.

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### EXPLANATION OF PLATES 25—27,<sup>1</sup>

Illustrating Prof. W. A. Haswell's paper, "Studies on the Turbellaria."

#### LIST OF REFERENCE LETTERS.

*a.* Atrium. *ant.* Antrum femininum. *b.* Bursa copulatrix. *bl.* Bulb of bursa seminalis. *b. m.* Basement membrane. *br.* Brain. *b. s.* Bursa seminalis. *b. s.<sup>1</sup>* Outer layer of wall of bursa seminalis. *b. s.<sup>2</sup>* Inner layer of wall of bursa seminalis. *b. s. d.* Duct leading from antrum to bursa seminalis. *c.* So-called cuticle. *ch.* Chitinous mouth-piece. *ch. c.* Cells secreting substance of chitinous mouth-pieces. *c. m.* Layer of circular muscular fibres of body-wall. *cp.* Capillary canals in epidermis. *c. w.* Cell-wall of Alga.

<sup>1</sup> Figures 7, 9, 10, 12, 13, 16, 21, 22, 26, 28, and 32 were drawn by Mr. A. Cronin, of the Physiological Department of Sydney University, from my photographs of sections, of which they are, to all intents and purposes, facsimiles.



*d.* Ducts leading to chitinous mouth-pieces. *d'*. Enlargements of ducts of mouth-pieces. *e.* Eye. *ent.* Enteric cavity. *ep.* Epidermis. *ex.* Main excretory vessels. *f.n.* Frontal nerves. *g.d.* Ducts of granule glands. *gl.* Unicellular glands opening into antrum. *g.r.* Granule reservoir. *i.* Intestine. *k.* Supposed passage by which the eggs are discharged. *l.m.* Longitudinal muscular fibres of body-wall. *l.n.* Lateral nerve. *mlh.* Mouth. *n.* Nucleus. *od.* Oviduct. *oo.* Oosperm. *ot.* Cavity in which otocyst lies. *ov.* Ovary. *p.* Penis. *ph.* Pharynx. *pl.* Polar body. *pr.* Processes connecting epidermal cells. *p.s.* Penis sheath. *rh.* Rhabdite-forming or other integumentary glands. *rh.d.* Ducts of integumentary glands. *r.s.* Receptaculum seminis. *sh.* Egg-membrane. *t.* Testis. *u.* Uterus. *v.* Vesicula seminalis. *x.* Position of supposed Laurer's canal. *z.* Group of cells behind brain. ♂. Male reproductive aperture. ♀. Female reproductive aperture.

## PLATE 25.

FIG. 1.—Outline of *Heterochærus* magnified 20 times to show the relative positions of the mouth and reproductive apertures.

FIG. 2.—Semidiagrammatic view of the general organisation. × 40.

FIG. 3.—Transverse section through the epidermis and underlying layers. × 1500.

FIG. 4.—Pigment cell of epidermis. × 1675.

FIG. 5.—Rhabdites. × 1500.

FIG. 6.—Symbiotic *Zoochlorella*. × 600.

FIG. 7.—Portion of a horizontal section passing through the digestive syncytium, showing large numbers of the *Algæ* in the more superficial layers of the latter. Facsimile of a photograph.

FIG. 8.—Portion of a transverse section passing through the mouth.

FIG. 9.—Horizontal section passing through the so-called pharynx and the main enteric cavity. Facsimile of photograph.

FIG. 10.—Horizontal section on a higher (more dorsally situated) plane than that represented in Fig. 8, showing the enteric cavity and the digestive plasmodium, with portions of the testes at the sides. Facsimile of photograph.

FIG. 11.—Central part of a similar section more highly magnified. The black dots are the nuclei of the plasmodium.

FIG. 12.—Anterior part of a horizontal section passing through the brain, the eyes, and the cavity in which the otocyst is enclosed. Facsimile of photograph.

## PLATE 26.

FIG. 13.—Horizontal section of *Heterochærus* showing a considerable part of the ventral nerve-plexus. Facsimile of photograph.

FIG. 14.—Part of a similar section to that represented in Fig. 12, more highly magnified.

FIG. 15 *a*.—Small sperm.  $\times 1500$ .

FIG. 15 *b*.—Head end of giant sperm.  $\times 1500$ .

FIG. 16.—Horizontal section in the plane of the ovaries, the bursæ, and their ducts. Facsimile of photograph.

FIG. 17.—General view (semidiagrammatic) of the left bursa seminalis with its duct and the antrum femininum.

FIG. 18.—Section through one of the chitinous mouth-pieces with its bulb and the wall of the bursa seminalis. From a horizontal section of the animal.  $\times 700$ .

FIG. 19.—Lateral view of some of the chitinous elements of the mouth-piece in their natural relations.

FIG. 20.—Isolated chitinous elements of the mouth-piece.

FIG. 21.—Approximately sagittal section, showing Laurer's canal (*x*). Facsimile of photograph.

FIG. 22.—Sagittal section, showing the relation of Laurer's canal in another specimen. Here the canal shows no distinct lumen, but its course is clearly indicated by the arrangement of the histological elements between the dorsal aperture (*x*) and the antrum femininum (*ant*).

FIG. 23.—Section through the fertilised ovum passing somewhat obliquely through the first cleavage spindle and through one of the polar bodies.  $\times 330$ .

FIG. 24.—Portion of a section through unfertilised ovum, showing appearance of chromatin elements after formation of polar bodies.  $\times 600$ .

## PLATE 27.

FIG. 25.—General view of the organisation of *Anomalocælus*, seen from the ventral aspect. The testes and the vitelline glands are not represented.  $\times 45$ .

FIG. 26.—Vertical section of the integument, showing transverse sections of some of the epidermal capillaries. Facsimile of photograph.

FIG. 27.—Vertical section through the epidermis.  $\times 1500$ .

FIG. 28.—Portion of a horizontal section of the epidermis. Facsimile of photograph.

FIG. 29.—Surface view of a part of an entire preserved specimen.  $\times 1500$ .

FIG. 30.—General view of the reproductive apparatus.  $\times 280$ .

FIG. 31.—Horizontal section passing through the ovary, receptaculum seminis, and uterus.  $\times 280$ .

FIG. 32.—Similar section on a somewhat higher plane. Facsimile of photograph.

FIG. 33.—Horizontal section passing through the vesicula seminalis and prostate reservoir.  $\times 280$ .

FIG. 34.—Teeth of penis. *a*, Larger; *b*, smaller.